# A GENUS OF PALAEARCTIC AND NEARCTIC FLEAS 

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# A CONTRIBUTION TO THE TAXONOMY OF STENOPONIA J. \& R. (igil), A GENUS OF PALAEARCTIC AND NEARCTIC FLEAS 

By KARL JORDAN

The original diagnosis of Stenoponia was based on the description and figures of Hystrichopsylla tripectinata Tiraboschi (1902) (designated type species), of which a male had been obtained at Rome on Mus musculus, and on a Chinese female off Sciurotamias davidianus consobrinus. This generic concept has since been much widened by the inclusion of Hystrichopsylla americana Baker (1899) and a number of new species described since 1925 .

When, in the spring of 1912, I913 and I914, I was in Algeria with Walter Rothschild I devoted some time to collecting mammals for the sake of their fleas. Stenoponia were found in three places: Hammam Meskoutine, west of Guelma, Khenchela, at the east end of the Aurès Mts., and at Guelt-cs-Stel, a bordj (castle) on the route from Boghari to Djelfa. Rothschild and Hartert went in 1913 to western Algeria mainly to collect birds, but they took with them Alan Ruddle of the Mammal Department of the British Museum (Natural History), who obtained a fine series of a Stenoponia at Djebel Mourdjadjo at the back of Port Oran, and of another Stenoponia at Aïn-Séfra, far south-west near the border of Morocco. The outbreak of the war in 1914 put an end to these yearly excursions. In 1920, however, Charles Rothschild and I spent some months in Algeria and on the way from Biskra south we observed from the platform of the railway carriage Jaculus hopping about in a flat area which was studded with bushes growing out of little hillocks of sand. Before proceeding to Touggourt we collected for some time at an intermediate place called Djama or Djamma, and here I caught for the first time Gerbillus hirtipes, which sleeps during the day in such dunes as just mentioned. I got only one gerbil and it had no fleas.

In our records of Mediterranean fleas we listed the Stenoponia from various places simply as S. tripectinata Tiraboschi, 1902, without mentioning any differences we had observed. It seemed to us advisable to postpone an analysis until more abundant collections from a greater number of localities would be available. What we had in the collection seemed to show the populations to intergrade and even to overlap to a remarkable extent. The publication of the description of S. insperata in 1930 by Weiss of the Pasteur Institute in Tunis therefore came somewhat as a shock, but induced us to look at our Stenoponia again. Weiss's account, however,
as well as what was said on the same Tunisian fleas soon after by Wagner (1930) and Wagner \& Wassilieff (1933) left me where I was before. They cleared away some muddles about locality and hosts of Tunisian S. insperata and S. tripectinata, but avoided the taxonomic difficulties by basing the definitions of their two " species " on the somatics of majorities and neglecting the minorities which are connecting links between populations. They state, for instance, of the antepygidials of S. insperata " ordinairement " in male 3, female 4. As this flea is said by them to occur at Bir Mellah in the nests of Meriones shawi in enormous quantity, it is quite safe to assume that there is a percentage with 4 in the male and with 5 in the female, the numbers in four pairs of a very similar Stenoponia from Rehoboth in Israel being in the male 7 sides with 3 and $I$ with 4 , and in the female 5 sides with 4 and 3 with 5 , and in a pair from Biskra there are 3 and 3 in the male and 3 and 4 in the female.
Much more stimulating than the Tunisian specimens are those now known from Egypt. I am profoundly grateful to Lt.-Col. Robert Traub for having entrusted me with a large number of mounted specimens of Stenoponia collected by Mr. H. Hoogstraal, to whom also I here express my gratitude. This remarkable collection emboldened me to write for assistance to Dr. O. Theodor, Dept. of Parasitology, Hebrew University, Jerusalem, who most generously responded by sending specimens and much information on the distribution of Stenoponia in Israel and their particular environment, for all of which I thank him most sincerely. When I learned from his communications that his department has a large collection of fleas (over 200 specimens of Stenoponia, for instance) obtained from different localities stretching from the north to the south of the country, most of them cleared and mounted, I was much astonished and greatly thankful for the opportunity to study some of them. From Iraq we have a pair kindly presented by our friend Dr. C. Andresen Hubbard and a second female collected by Dr. D. L. Harrison. The other countries of the Middle East, Syria, Lebanon, Jordan and Saudi Arabia, are as regards this enquiry complete vacua.
Section I.-Asiatic and Nearctic species. Genal comb with one angle (at base of spines 4 and 5 , last (uppermost) spine in a line with the preceding ones, never projecting over the antennal fossa.
Subsection A ${ }^{1}$.-Smallish species from the Pacific area of Palaearctic Asia. Genal comb with $9-12$ spines. Oral margin less than half as long as the genal comb ( 36 : $100 \pm$ ). Pronotum inclusive of comb as long as metanotum (measured dorsally) or at most one-fifth longer. All tarsi of both sexes with 4 spiniforms on apical area of ventral surface.
む. Apex of IX.st. not or feebly widened, more convex dorsally than ventrally. Ventral sclerite of phallosome without armament, not bearing the inverted claw present in all $\delta^{t}$ of Subsections $\mathrm{A}^{2}$ to $\mathrm{A}^{5}$.
아. Posterior margin of VII.st. straight at least in its ventral third, without distinct sinus. Body of spermatheca oviform, dorsal and ventral margins evenly curved and of the same length, orifice of duct central, no transverse sclerotized stripe defining the sort of snout present in all other species of the genus.
Four species known.

## I. Stenoponia coelestis J. \& R., I9II

Labial palp with one segment, which reaches to the end of the maxillary palp. Number of spines in the genal comb 9 on both sides in the holotype, Io/Io in the second specimen. Pronotum inclusive of comb one-tenth longer than metanotum. Pronotal comb with I8 (or I9?) spines each side. On terga IV to VI of abdomen two rows of bristles and no additional bristles in front of them. Marginal spinelets on terga II to VI $7 / 8,6 / 7,4 / 5,3 / 5,0 / \mathrm{I}$. Stylet with one long bristle at apex. The longest apical bristles of hind tarsal segments I and II not reaching to the apex of the segment following.

Habitat. South-east of Ta-tsien-lu, West China, I $\&$ from Sciurotamias davidianus consobrimus (Anderson leg.), another female (without abdomen) from Si-ho River, western Szechwan, off Microtus alcinous (now Clethrionomys rufocanus shanseius), presented by Oldfield Thomas, both in the Brit. Mus. (Nat. Hist.) collection at Tring.
2. Stenoponia formozovi Ioff \& Tiflov (1934, \& ; Ioff \& Scalon, 1954, © )

Labial palp with one segment. Number of spines in genal comb in four males Io/IO, IO/II, II/IO, II/II, in seven females twice IO/IO, once II/IO and four times II/II. Pronotal comb of female with 50 spines on the two sides together. Pronotum only I unit* longer than metanotum. Number of antepygidials in four males $3 / 3$, in eight females seven times $4 / 4$ and once $5 / 4$.
o. Distal half of ventral arm of IX.st. narrower than proximal half.

ㅇ. Posterior margin of VII.st. entire, vertical.
Habitat. Amurland and Transbaikalia. Not in the Brit. Mus. (Nat. Hist.) collection. Additional information received from Dr. V. E. Tiflov and used here.

## 3. Stenoponia montana Darskaya, 1949

Labial palp with two segments. Number of spines of genal comb in male 10/10, in female $12 / \mathrm{I} 2$, of pronotal comb in male $19 / \mathrm{I} 9$, in female $25 / 23$, of comb of abdominal tergum I in male $16 / 16$, in female $21 / 20$. Spinelets of abdominal terga II to VI in male $7 / 6,5 / 6,5 / 4,3 / 3$, o/o, in female $8 / 8,7 / 6,6 / 6,4 / 5$, o/o. Antepygidials in male $3 / 3$, in female $4 / 4$. On abdominal terga IV to VI two rows of bristles and some small additional ones.

む. Ventral arm of IX.st. a little narrower distally than in middle ; apex of paramere broad, with a curved-down hook in lateral aspect on slide.

ㅇ. Stylet with one long bristle at apex. VII.st. with lower area projecting as a broad lobe which is more or less slightly incurved.

Habitat. North Korea, on Clethrionomys rutilus; Nagano District, Japan, I,500 m., November 1953, on Apodemus speciosus. One pair in Brit. Mus. (Nat. Hist.) from Nagano, presented by Dr. E. W. Jameson.

[^0]
## 4. Stenoponia sidimi Marikovsky, I936

Like S. montana, but easily distinguished by sexual somatics. Some of the bristles on the underside of the apex of IX.st. of male stout and shortened, spiniform ; apex of paramere resembling a helmet with a domed crown, the posterior margin having a rounded projection directed obliquely downwards. Stylet with several long bristles at and near tip.

Habitat. Kumwha, Korea, from Apodemus agrarius, Apodemus speciosus and Rattus norvegicus. Ussuri District, on Muridae, accidentally on Eutamias, Cricetulus and Mustela. In the collection of the Brit. Mus. (Nat. Hist.) 3 pairs from Korea presented by Lt.-Col. Robert Traub.

Subsection $\mathrm{A}^{2}$.-Nearctic species. Pronotum inclusive of comb at least one-third longer than metanotum. Oral margin shorter than longest spine of genal comb. Abdominal spinelets more numerous than in other species.
o. IX.st. widened at apex, its dorsal surface appearing straight ; as in all the following species of Section I, the ventral sclerite of the paramere with a sharp claw (each side) gradually curving upwards.
ㅇ. Stylet with one long bristle at apex.

## 5. Stenoponia americana (Baker), 1899

Bristles on frons above oesophagus all minute ; on metepimere only two rows of bristles, the subapical row (below the comb of abdominal tergum I) absent; all tarsi of both sexes with two apical spiniforms on ventral surface of segment V. These three distinctions do not occur elsewhere in the genus. Number of spines in the genal comb varying in male from $\mathrm{I} 2 / \mathrm{II}$ to $\mathrm{I} 4 / \mathrm{I} 4$ and in female from $\mathrm{I} 2 / \mathrm{I} 2$ to $\mathrm{I} 4 / \mathrm{I}_{5}$. The aggregate of spinelets on abdominal terga II to V (VI has no spinelets in this subsection) varies in our series from 7 I to 95 in the males and from 76 to 118 in the females. The usual number of antepygidials is $4 / 4$ in the male and $5 / 5$ in the female, but $4 / 3,4 / 5$ and $5 / 4$ also occur in the male and $5 / 6$ and $6 / 5$ in the female. Setose area of VIII tergum widely interrupted below stigma.

Habitat. Canada and U.S.A. south to Alabama, but we have not seen any specimens from the western area (Oregon southward to Colorado and Arizona) and it is not recorded from this area.

## 6. Stenoponia ponera Traub \& Johnson, 1952

On frons above the oesophagus the usual row of six or seven medium-sized bristles present. Labial palp long, consisting of at least two segments. Pronotum with two rows of bristles and one or a few small additional bristles which represent the third (anterior) row of S. americana. Genal comb with 14 or 15 spines according to the description, in our male and two females $14 / \mathrm{I} 4$. Antepygidials in male $4 / 4$, in our females $5 / 5$ and $6 / 6$. Spinelets of abdominal terga II to V less numerous than in S. americana, the aggregate being in the male 7 I and in the females 52 and

60 ; the comparatively low numbers in the females are rather surprising. On mesepimere below the frame of second spiracle four or more long bristles instead of two or three. Pale area of metepisternum horizontally shorter than vertically broad. Metepimere with three rows of bristles. Segment V of all tarsi, both sexes, with two pairs of spiniforms on the apical ventral area.
t. Widened apical area of IX.st. more densely setose than in S. americana and somewhat broader.

ㅇ. VII.st. without distinct ventro-lateral sinus and the setose area of VIII.t. not interrupted below spiracle.

Habitat. New Mexico, on Peromyscus and Eutamias; Durango, Mexico.
In Brit. Mus. (Nat. Hist.) I from Pinos Altos, New Mexico and 2 早from Durango, presented by Lt.-Col. Robert Traub.

Subsection A ${ }^{3}$.-Western Siberia and Kazakhstan, group III of Ioff \& Tiflov, 1934, containing two species, neither of which is represented in the British Museum. My notes on them are based on what the authors have published and on additional information most kindly given me by Dr. V. E. Tiflov.

Labial palp with two segments. Eye feebly pigmented. Oral margin longer than one-half the genal comb. Pronotum inclusive of comb as long as, or longer than, the metanotum measured dorsally. Number of spines of genal comb in males io/io, io/II, II/Io, II/II, in females io/iI, II/io, II/II, II/I2, I2/II, I2/I2, I2/I3. Antepygidials in males 3/3, 4/3, 4/4, in females $4 / 5,5 / 4,5 / 5,5 / 6,6 / 5,6 / 6,6 / 7,5 / 7$.
万. Digitoid ( F ) shorter than manubrium ( M ) of clasper, inserted farther upwards than in next subsection ; paramere with subapical narrow beak pointed and curved down ; apex of ventral arm of IX.st. strongly widened.
ㅇ. Margin of VII.st. with deep subventral sinus, the lobe below it projecting much more than the one above it.

## 7. Stenoponia ivanovi Ioff \& Tiflov, I934

Genal comb in fourteen males once $10 / \mathrm{IO}$, twice II/Io, eleven times II/II, in sixteen females once $10 / 11$, once $\operatorname{II} / \mathrm{IO}$, seven times II/II, twice $12 / \mathrm{II}$, and five times I2/I2, i.e. in males 4 sides with io and 24 with II, in females 2 sides with Io, I8 and II, and I2 with I2. Antepygidials in males eleven times $3 / 3$, twice $4 / 3$, once $4 / 2$, in females twice $5 / 4$, nine times $5 / 5$, once $5 / 6$, twice $6 / 5$, twice $6 / 6$, i.e. in males 24 sides with 3,3 with 4 , I with 2 (which is quite exceptional in the genus).
${ }^{\top}$. Manubrium ( M ) of clasper boat-shaped, being widened ventrally in middle, a little more than four times as long as it is broad at the widest point. Digitoid ( F ) one-sixth shorter than m , its anterior margin apically distinctly slanting distad. Widened apex of IX.st. obtusely angulate at upper and lower sides, the upper angle slightly more distinct than the lower one.

우. VII.st. with a deep subventral sinus, which is separated by a prominent lobe from a broader, rounded, second sinus, above this a shorter lobe.

Habitat. Western Siberia: west of Minussinsk and near Urda in Kazakhstan, on Lagurus lagurus, Cricetulus migratorius, and in nests of Microtus arvalis.

## 8. Stenoponia suknevi Ioff \& Tiflov, 1934

Genal comb in seven males twice $10 / \mathrm{IO}$, twice $\mathrm{IO} / \mathrm{II}$, once $\mathrm{II} / \mathrm{Io}$ and twice $\mathrm{II} / \mathrm{II}$, in ten females twice II/IO, four times II/II, twice II/I2, twice I2/I3, i.e. in males 7 sides with Io and 7 with II, in females 2 with IO, I2 with II, 4 with I2, and 2 with 13. Antepygidials in males once $3 / 3$, once $4 / 3$ five times $4 / 4$, in females once $4 / 5$, four times $5 / 5$, and once each $5 / 6,6 / 5,5 / 7,6 / 6$ and $6 / 7$, i.e. in males 3 sides with 3 , II with 4 , in females I with 4, I2 with 5,5 with 6 and 2 with 7 .
§. Manubrium ( $M$ ) of clasper slender, little widened in middle ; digitoid ( $F$ ) shorter than in $S$. ivanovi, only two-thirds the length of $m$, much broader at base, more curved, apex rounded; ventral arm of IX.st. narrower, the widened apex not angulate, the upper surface extending much farther distad than the lower, which is evenly and very moderately convex.
ㅇ. VII.st. with a deep and very narrow subventral sinus, at some distance above which the margin bears a small indentation, no second sinus. Spermatheca much less broad than in S. ivanovi.

Habitat. Eastern Kazakhstan, on Microtus arvalis.
Subsection A4.—Ashkhabad, Djarkent and Ust-Urt. Rather large fleas. Labial palp with two segments, basal one short. Eye pigmented. Pronotum inclusive of comb one-fifth to one-quarter shorter than metanotum. Anterior section of mesosternosome divided by an internal band-like incrassation which extends from the lower end of the meral rod obliquely upwards and forwards to the anterior margin of the segment, the upperside of the band more or less well defined, whereas its underside gradually fades away (this band indicated in some of the preceding species). Transparent area of metepisternum longer than vertically broad. Oral margin less than twice as long as longest spine of genal comb. Antepygidials in males $4 / 4$, in females $5 / 5,6 / 5$ and $6 / 6$.
$\delta^{5}$. Digitoid ( F ) of even width from near base to apex, which is rounded, longer than manubrium ( m ) of clasper.
ㅇ. On VIII.t. above spiracle on each side about a dozen bristles, of which four or five posterior ones are stout and long.

## 9. Stenoponia vlàsovi Ioff \& Tiflov, 1934

Genal comb more acutely angulate than in other species. Metepimere with four rows of bristles, the anterior one usually incomplete. Segment V of all tarsi (both sexes) with eight spiniforms on the apical half of the ventral surface (probably variable). Spinelets on abdominal terga in the aggregate in male 23, in females 23-37.
\$. Manubrium of clasper slightly boot-shaped, proportions $30: 7$. Lower margin of ventral arm of IX.st. extending farther distad than upper margin. Proximal end of plate of phallosome round, not pointed, not curved up, as broad as the plate is in middle (pathological ?).

ㅇ. VII.st. of abdomen with a broad shallow subventral sinus deepest below middle, the lobe above the sinus rounded, broad. Spermatheca much smaller than in $S$. conspecta.

Habitat. Ashkhabad, from nests of Spermophilopsis leptodactylus.
In the Brit. Mus. (Nat. Hist.) collection, a male and female from Ashkhabad off Rhombomys opimus, presented by I. Ioff, 3 q from Djarkent on Meriones tamariscinus (Rückbeil leg.).

## 10. Stenoponia conspecta Wagner, 1926

§ Stenoponia solitaria Ioff \& Tiflov, 1934, Rev. Microbiol., Saratov, 12, pp. 201, 204, 206, fig. 10.
Metepimere with three rows of bristles, with one or two additional bristles between the rows. Segment V of all tarsi (both sexes) with three pairs of spiniforms ventrally on the apical area. Aggregate of abdominal spinelets in males 42 and 62, in females 50 and 60.
$\delta^{\top}$ Manubrium of clasper broadened, proportions 30:9-10 (in figure of solitaria a little broader). Digitoid (F) more curved than in S. vlasovi. Apical dilatation of IX.st. nearly as in S. suknevi, the upper margin extending farther distad than the ventral one, the extreme apex being dorsal.

ㅇ. Subventral sinus of VII.st. deepest near its upper end, the lobe bounding it pointed. Tail of spermatheca broader than in $S$. vlasovi, snout more prominent, body almost as broad as long.

Habitat. Djarkent and Ust-Urt, on Rhombomys opimus.
In Brit. Mus. (Nat. Hist.) 2 ô and 2 f from Ust-Urt, presented by I. Ioff, and I $\widehat{0}$ from Djarkent.

Subsection $A^{5}$.-The single species, from Transbaikalia, differs so much from all the others that it might be advisable to place it in a separate genus. The male and female in the British Museum collection are defective, but show clearly some remarkable distinctions. The spines of the three combs much shorter than usual. Oral margin much longer than elsewhere, at least three times as long as the longest genal spine and nearly as long as the genal comb. Pronotum inclusive of comb shorter than metanotum.

## r1. Stenoponia singularis Ioff \& Tiflov, 1934

A large species. Genal comb with $\mathrm{I} 2-\mathrm{I} 4$ spines (Ioff \& Tiflov), in our male genal comb II/I2, in female $13 / 13$. Labial palp with one segment, which is longer than the fourth segment of the maxillary palp. First segment of the latter nearly one-half longer than II and III together, which are shorter than usual. Bristles of segment II of the antenna more than eight, especially long and numerous in female. Pronotum with two rows of bristles. Band-like incrassation dividing the anterior section of mesosternosome sharply defined, sclerotization of underside of band concentrated into a stripe extending downwards. Legs shorter than in any other species, particularly the tarsi, segment IV of hind tarsus being only one-eighth and V one-half
longer than broad (pedicel excluded), III of hind tarsus in S. vlasovi and S. conspecta more than thrice as long as apically broad, in S. singularis the proportions are in male $20: 10$, in female 15 : 10. Antepygidials in our male $5 / 4$, in female $6 / 7$. Sensilium of male transverse, twice as broad as long, in female a little broader than long and not convex as in all other species of the genus. Abdominal spinelets in male too defective, in female on IV $8 / \mathrm{II}, \mathrm{V}_{5} / \mathrm{mo}$, VI $1 / 0$.
万. Digitoid ( F ) of clasper the shortest in Stenoponia, the apical third of its anterior margin slanting backwards, the tip of the digitoid obtusely pointed.

ㅇ. VIII.t. above spiracle with nine or ten long stout, straight, bristles (besides many smaller ones) each side. Stylet with three long bristles at apex. Spermatheca stout, body one-third longer than broad.
Habitat. Transbaikalia, on Myotalpa (now Myospalax) myospalax.
In Brit. Mus. (Nat. Hist.) one pair, presented by I. Ioff.
Section II.-The Stenoponia tripectinata complex, ranging from the Azores to Iraq. The following account is based on some 180 specimens, mounted in Canada balsam, and on the detailed information most kindly given me by Professor 0. Theodor on the distribution, hosts and geophysical environment of the various Stenoponia occurring in Israel. The main distinction of the tripectinata complex from Section I is the gradual extension of the genal comb along the antennal fossa. A specimen which shows no indication of this development can always be recognized as belonging here by some other general somatic difference: the labial palp consists always of one segment ; the oral margin and first segment of the maxillary palp are of approximately equal length, and the anterior area of the mesosternosome is divided by a well-defined band-like sclerotization into an upper and a lower portion (nearly as in S. singularis Ioff \& Tiflov).

Although the lower extreme of variation, without the second angle of the genal comb, is in several parts of the body very different from the upper extreme, with 4 spines along the antennal fossa and the eye consequently pushed upwards to the level of the oesophagus, a division of the available material into definite populations of closely related specimens leaves a residue of individuals which take an intermediate position. There is even some uncertainty about specimens taken off the same host-individual : it is reasonable to assume that these are members of one brood, i.e. brothers and sisters, but their morphological differences may be due to mixed parentage and certainty can only be attained by breeding. The knowledge of the genetics of at least one population of Stenoponia is greatly to be desired for another reason also. About a dozen females of various species (Nearctic, Asiatic and Mediterranean) contain one or two eggs (or remnants of eggs) each (Weiss, 1930, pl. 5), though never more than two ; they are so large that the two of them occupy about three-fifths of the lumen of the abdomen (Text-fig. I). The sclerites of the abdominal segments are not broken up, nor are the intersegmental membranes enlarged, but there is a special adaptation in the eighth tergum for facilitating the passage of such a large egg, the posterior portion of the segment bearing a fold or slit running some distance forwards from the margin,


Fig. 1. Stenoponia tripectinata acmaea ssp. nov. Sketch of abdomen of female, El Mansuriva, Giza Province, Egypt, to show relative size of eggs.


Fig. 2. Stenoponia tripectinata tripectinata (Tiraboschi). Head of male, Asuni, Sardinia. entom. 6, 7 .
which permits the segment to expand. This arrangement and its function would be worth study when breeding experiments are carried out.

Subsection $\mathrm{B}^{1}$.-Above the point where the left and right oral margins meet there is a more or less distinctly projecting angle (oral angle) (Text-fig. 2; for lettering see Text-fig. 3, A) ; the distance (AC) of a from the base of the uppermost spine of the genal comb (c) is longer than the oral margin (CD). The total number of spinelets on abdominal terga II to VI, counting both sides together, is more than 30 in both sexes.


Fig. 3. Stenoponia tripectinata acmaea ssp. nov. Head of male paratype, El Mansuriya, Giza Province, Egypt.

Group $b^{1}$.-We unite here all the populations in which at most one spine is moved upward at the antennal fossa out of line with the preceding ones. Pronotal comb varying in the male from 35 to 40 spines (average 37) and abdominal comb from 32 to 38 spines (average 35 ) ; in the female the pronotal comb from 36 to 43 spines (average 37) and abdominal comb 35-4I (average 35).

## 1. Stenoponia tripectinata tripectinata Tiraboschi, 1902

The nomenclatorially typical (or nominate) subspecies is, in this case, also the most primitive one. AC longer than CD (Text-fig. 2). Variation of genal comb in



6


9


7


10


8


II

Figs. 4-ir. Genal comb in specimens of various subspecies of Stenoponia tripectinata. 4, 5. Left and right sides, respectively, of a male S. t. tripectinata from HammamMeskoutine, Algeria. 6. Female S. t. tripectinata, St. Michael, Azores. 7. Male holotype of S. t. tenax ssp. nov. 8. Male paratype of S. t. megaera ssp. nov. 9. Male paratype of $S$. $t$. tingitana ssp. nov. Io. Male paratype of S. t. tingitana ssp. nov. II. Female paratype of S. t. acmaea ssp. nov.
male II/I2, I2/II (Text-figs. 4, 5) , I2/I2, I2/I3, I3/I2, I3/I3, in female II/I2, I2/II, I2/I2, I2/I3, I3/I2, I3/I3, I3/I4, I4/I3, I4/I4 (Text-fig. 6) ; of antepygidial bristles in male $3 / 3,3 / 4,4 / 4,4 / 5$, in female $4 / 4,5 / 4,5 / 5$. Total number of abdominal spinelets of each individual varying in male from 49 to 70 (average 59) and


Fig. 12. Stenoponia tripectinata tripectinata (Tiraboschi).
Terminalia of male, Asuni, Sardinia.
and in female from 42 to 67 (average 54). Number of small spiniforms on apical area of underside of tarsal segment $\mathrm{V}^{*}$ varying in male on fore and mid tarsi from 6 to 9 (usually 6 or 7 ), on hind tarsus $4-6$ (average $5 \cdot 2$ ), in female on fore and mid tarsi from 4 to 6 (usually 5), on hind tarsus from 2 to 5 (usually 4).

[^1]In the male (Text-figs. 12, $15-17$ ) the widened apical portion of the morphologically ventral branch of IX.st. bent backwards, contrasting in direction with the narrow proximal portion of the branch and varying much in the degree of convexity of the upperside ; the sclerite (crotchet plate) placed at the side of the terminal tube of the ejaculatory duct varies in size and shape in this and nearly all other populations of tripectinata, usually bearing a longish crotchet at the lower angle pointing obliquely down and sometimes a short one at the upper angle ; subapical lobe of paramere more or less curved down at end. Abdominal tergum VI of male with one


Figs. 13, 14. Combs of abdomen in males of Stenoponia tripectinata sspp. 13. S. t. tripectinata (Tiraboschi), Hammam-Meskoutine, Algeria. 14. S. t. megaera ssp. nov. holotype.
or more spinelets, most of which are lateral, situated above the spiracle of VII.t., which shines through VI (Text-fig. I3).

Habitat. St. Michael, Azores, roth March, 1903, on Mus (probably " mouse '"), W. R. Ogilvie-Grant, 4 ; Porto Santo, Madeira, T. V. Wollaston, I 9 ; Asuni, Sardinia, 1910, on Mus (probably "Maus" = mouse) and under a stone, A. H. Krausse, 2 đ̉, 3 早; Portici, S. Italy, 1917, on Pitymys savii, Dr. Nello Mori, I 9 ; Malcoci, Romania, 19th December, 1906, on Mus (probably " mouse "), A. Rettig ; Dobrogea, Romania, 1913, on Apodemus sylvaticus, W. Facius, I 9 ; Adana, S. Anatolia, Turkey, January, 1907, on Mus musculus, and March 1907, on Sorex sp., B. H. Boyadjian, 7 ơ, 6 우; Khenchela, east end of Aurès Mts., Algeria, May

1912, on "Mus algirus" (error for Mus musculus, wild form), K. Jordan, 7 or $^{\text {T, }}$ 3 우; Hammam Meskoutine, west of Guelma, Algeria, April 1914, on Mus musculus (wild form) and Arvicanthis (now Lemniscomys) barbarus, K. Jordan, 9 d', ro 9.

Considering that the extent of the variation of the topotypical population of this unstable flea is not known (the holotype, from Rome, having perished and there being in the British Museum collection only a single nearly topotypical female, from Portici), and that we have only one or a few specimens from six of the nine places mentioned above, splitting up Group b1 into several subspecies would be premature. The analysis of the characters of the twenty-six males and twentynine females here recorded hints at the possibility that, on receipt of adequate collections from a greater number of localities in the large area in which this flea occurs, one or two new subspecies may become definable. The percentages of males with different numbers of antepygidial bristles ( 3,4 or 5 ) suggest the following combinations of localities: (I) Azores, Madeira, Sardinia, Italy, Moldavia and other localities north of the Mediterranean Sea (in male $87 \%$ with 4 and $13 \%$ with 5, none with 3). (2) Algeria (Hammam Meskoutine and Khenchela) (in male 10\% with 3 and $90 \%$ with 4 , in female $100 \%$ with 5). (3) Adana (in male $50 \%$ with 3 and $50 \%$ with 4 , in female $50 \%$ with 4 and $50 \%$ with 5 ; moreover, the extreme of dorsal convexity of the club-end of IX.st. of the male occurs (Text-fig. 17) in the Adana series.

Group $\mathrm{b}^{2}$.-Two spines at the upper end of the genal comb are above the alignment of the comb. Three subspecies.

## 2. Stenoponia tripectinata tenax subsp. nov.

In our few specimens (three males, one female) the labial palp of the male is approximately one-fifth shorter than the first segment of the maxillary palp and one-eighth shorter than the oral margin, in the female one-fourth and one-fifth respectively, the proportion in numerals (labial palp $=\mathrm{I}$ ) in male $\mathrm{I}: \mathrm{I} \cdot 23$ and $I: I \cdot I 3$, and in female $I: x \cdot 3 I$ and $I: I \cdot 25$. The width $A C$ of the ante-antennal (frontal) section of the head varies from a little shorter to a little longer than one and a half times the oral margin (AD), the proportions being I: $1 \cdot 48$ in male and I : 1.55 in female ; AD shorter than $B D$. Variation of genal comb in male $\mathrm{I} 2 / \mathrm{I} 3$ (holotype, Text-fig. 7), $13 / \mathrm{I} 2, \mathrm{I}_{3} / \mathrm{I} 2$, in the single female $13 / \mathrm{I}_{3}$. Antepygidials in male $3 / 3,3 / 3,3 / 4$, in female $5 / 5$. Number of spines in pronotal comb of male 35-36, and in abdominal comb 30-33 (these numbers a little lower than in S. t. tripectinata) ; in female pronotal comb with 36, abdominal comb with 38. Total number of abdominal spinelets in the three males 50,56 (average 54), in the female 54 (more than in the following subspecies) ; the spinelets on tergum V of the males number $6 / 6,6 / 6$ and $7 / 7$, those on VI $1 / 3$, o/r (lateral) and $r / 0$, in the female $5 / 6$ on V . Spiniforms on apical area of underside of tarsal segment V more numerous than in S. $t$. tripectinata, in male on fore tarsus 8 -r3 (average $9 \cdot 8$ ), mid tarsus 10-12 (average II•3), hind tarsus 6-8 (average 6.4), in female 7,6 and 6 .


Figs. 15-25. Expanded apical part of ninth sternum in males of different subspecies of Stenoponia tripectinata. 15, 16. S. t. tripectinata (Tiraboschi), Hammam-Meskoutine, Algeria. 17. S. t. tripectinata (Tiraboschi), Adana, Anatolia, Turkey. 18. S. t. tenax ssp. nov., paratype. 19. S. t. barcana ssp. nov., holotype. 20. S. t. tingitana ssp. nov., holotype. 21. S.t. tingitana ssp. nov., paratype. 22. S. t. insperata (Weiss), Bir Mellah, Tunisia. 23. S. t. separata ssp. nov., holotype. 24. S. t. thinophila ssp. nov., holotype. 25. S. t. acmaea ssp. nov., paratype, El Mansuriya, Giza Province, Egypt.
IX.st. of male similar to that of S.t.tripectinata, broken off and lost in one specimen, longer and the dorsal side less incurved in the other paratype than in the holotype (Text-fig. 18) ; lower angle of crotchet-plate in two males with a fairly long crochet directed downwards, upper angle effaced, in third male the crotchet plate similar to that of Text-fig. 26 but smaller, the lower crotchet shorter and the upper one more distinct; subterminal lateral lobe of the paramere curved down at the end.

Habitat. Guelt-es-Stel, roughly midway between Boghari and Djelfa, Algeria, $3 \sigma^{\star}$ (including holotype) on 23rd April, 1912, and I ㅇ on 21st May, 1912, off Meriones shawi, K. Jordan. This is the only place on the high plateau westward of Batna from which we have any fleas.


Fig. 26. Terminalia of male holotype of Stenoponia tripectinata megaeva ssp. nov.
3. Stenoponia tripectinata megaera subsp. nov.

The definition of this subspecies is based on the specimens from Djebel Mourdjadjo, Oran. Labial palp longer than in S. tripectinata tenax, as long as the oral margin or a fraction shorter, taking its length as $I$, the proportions with the first segment of the maxillary palp and with the oral margin are in the male $1: 1.07$ and $1: 0.97$, and in the female $I: I \cdot 04$ and $I: I \cdot O I$. Variation of the genal combs in the male II/II (Text-fig. 8), two with $12 / 12$, two with $12 / 13$, in female II/I2, four with

I2/I2, five with I3/I3, two with I4/I3. Width AC of frontal portion of head usually one-half longer than AD , the difference very rarely sinking to four-elevenths of AD . As in S. tripectinata tenax, AD is smaller than BC and is less than half BD. Antepygidials in our males $4 / 4$, in eleven of the twelve mounted females (one defective)


Fig. 27. Tip of abdomen of female of Stenoponia tripectinata megaera ssp. nov.
three with $5 / 5$, one with $6 / 5$, five with $6 / 6$, one each with $7 / 6,7 / 7$; the prevalence of six and seven in a set of antepygidials ( $68 \%$ against $32 \%$ with five) characterizes this subspecies, the high numbers not occurring elsewhere in the $S$. tripectinata complex except in Morocco. Total numbers of abdominal spinelets varying in the males from 4 It 49 (average 47), in the females from 36 to 52 (average 43). Spinelets on V.t. in male $3 / 2,4 / 4,4 / 2$ (Text-fig. 14), 4/4, 3/3 (average of totals for both sides 6.6,
much lower than in S. tripectinata tenax, for which it is 12.7 ), on VI.t. three with I/0, twelve with $I / I$, in female spinelets on V.t. varying from $I / I$ to $4 / 4$ (average of totals $4 \cdot 83$ ). Spiniforms on apical area of underside of segment $V$ of fore and mid tarsi 6-10 (average 8.5), on hind tarsus 5-6 (average 5.3), in female on fore and mid tarsi 6-8 (average 7 ), on hind tarsus $4^{-6}$ (average $5^{5}$ ).

In the male (Text-fig. 12) the enlarged apical part of IX.st. dorsally more or less strongly convex, its apical margin slanting downwards and backwards, the most distal point being ventral or subventral ; subterminal lobe of paramere not turned down at end, lower crotchet exceptionally long, straight, upper one short.

Female with tip of abdomen as in Text-fig. 26. Spermatheca (Text-figs. 27, 28) very variable in length of tail, distance between two parallel lines, one touching the tail at the anterior curve and the other at the tip, $16-22$ units.

Habitat. Djebel Mourdjadjo (behind Port Oran), Oran Province, Algeria, April 1913, on Dipodillus campestris, Alan Ruddle, 5 ô (including the holotype), 129.


28


29

Figs. 28, 29. Spermatheca in female paratypes of Stenoponia tripectinata megaera ssp. nov.

Five males and three females, recently received from the Pasteur Institute at Casablanca and collected off Dipodillus campestris in the Nefifik Forest 33 km . NE. of Casablanca by Dr. J. Bruneau, are very similar to the Mourdjadjo population, but in all eight specimens the left genal comb has the same numer of spines as the right one, instead of three heads being asymmetrical in the combs as identity would demand. That raises the question whether the specimens with genal combs arranged symmetrically (like II/II and $12 / \mathrm{I} 2$ ) are to be treated as taxonomically identical with the asymmetrical ones ( $\mathrm{II} / \mathrm{I} 2$ and $\mathrm{I} 2 / \mathrm{II}$ ). The point will be dealt with in Subsection B2, where asymmetry of this kind is conspicuous. The series from Morocco further differs in the antepygidials of the five males consisting of three sets of 3 and seven of 4 , whereas in the Oran males they are all sets of 4 ; in the three Moroccan females they are $6 / 6,6 / 5$ and $5 / 4$, none with 4 occurring in our twelve Oran females. Moreover, in this female with $5 / 4$ there is on the left side of VI.t a distinct spinelet, the specimen being the only exception in our collection to the rule that in the S. tripectinata complex VI.t. has no spinelet in the female, and there is the additional difference that the average of spinelets on
V.t. is in the males $7 \cdot 6$ and in the females $6 \cdot 0$, as compared with the Oran averages of 6.6 in male and 4.8 in female; variation in the individual totals of spinelets in the males is $40-52$ (average 47), in females 36-49 (average 41, the high number in the aberrant third female). The distinctions are of no great weight and they may be negatived on receipt of more Moroccan material ; perhaps they indicate only that the eight specimens deviate partially from the Oran series, and for the time being, therefore, they may be referred to as Moroccan megaera.

## 4. Stenoponia tripectinata barcana subsp. nov.

Forehead shorter than in the three preceding subspecies, approaching in proportions the Gerbillus-flea of Subsection B2 ${ }^{2}$. Frontal tubercle not quite effaced; in male AC (measured both sides, 27/28 and 29/26) at most one-eighth longer than AD and AD a fifth longer than BC and less than two units longer than half $\mathrm{BD} ; \mathrm{CD}$ equal to AD or one unit longer. Labial palp as in S. tripectinata megaera, somewhat longer than in S. tripectinata tenax. Genal combs in males II/II and $12 / \mathrm{I} 2$, in both females I3/I3. Antepygidials in both males $3 / 3$, in females $4 / 4$ and $5 / 5$. Pronotum inclusive of comb as long as metanotum or one unit shorter. Totals of abdominal spinelets in males 32 and 44, in females 36 and 43, the averages ( 38 and 39.5) lower than in tenax and megaera. Males with spinelets on V.t. $3 / 2$ and $5 / 3$, on VI.t. o/o and $\mathrm{r} / \mathrm{o}$. Spiniforms on apical area of underside of segment V of tarsi in male 9 -Io on fore and mid tarsi, 6 on hind tarsus, in female 6 on fore tarsus, 5 and 6 on mid tarsus, 4 and 5 on hind tarsus.

Dilated apex of ventral arm of IX.st. of male (Text-fig. 19) rather strongly convex on the upperside, apical margin rounded, without angle, most distal point below middle, rather closely resembling Text-fig. 17. Crotchet-plate small, crotchets vestigial. Heel of manubrium of clasper gradually widened, less abruptly than in megaera.

The slanting upper margin of the lobe above the subventral sinus of VII.st. of the female somewhat abruptly incurved.

Habitat. Barca (or Barka) peninsula, Cyrenaica, Libya, April 1946, on Spalax ehrenbergi aegyptiacus, Major W. Scott, two pairs (holotype a male).

Group $\mathrm{b}^{3}$.-Three or four spines of the genal comb placed at the margin of the antennal fossa, sometimes the base of the lowest of these spines not completely above the preceding one. The number of spines in the genal combs varies in the male from II to 14 (not 15 ) and in the female from I3 to 15 (but 15 occurring only on one side of very few specimens). Pale area of metepisternum always distinctly longer than vertically broad. AD smaller than half BD and equal to BC ( $\pm \mathrm{I}$ or 2 units), AC one-sixth to a half longer than AD , usually one-third or a quarter.

## 5. Stenoponia tripectinata tingitana subsp. nov.

Labial palp less than two-thirds the length of oral margin. Genal comb in male 12/I2 (Text-fig. 9), two with 13/14, 14/14 (Text-fig. 10), in female 14/I3. Pro-
notum inclusive of comb a little shorter than metanotum (12:13 in male, $14: 17$ in female, $\pm \mathrm{I}$ ). Spines in pronotal comb in male 33-36 (average $34 \cdot 25$ ), of abdominal comb $30-34$ (average 31), in female 37 and 36 . Variation of totals of abdominal spinelets in males $34,50,29,36$ (average $37 \cdot 25$ ), which is less than in the four preceding subspecies) ; in female 36. In male spinelets on V.t. 3/1, 4/2, $\mathrm{o} / \mathrm{I}, \mathrm{I} / \mathrm{I}$, total 13 (a low number), on VI.t. $\mathrm{I} / \mathrm{o}$ and three with o/o ; in female on V.t. $2 / 3$, on VI.t. o/o. Antepygidials in males three with $3 / 3$, one with $4 / 4$, in female $5 / 5$. Spiniforms on apical area of underside of segment V of tarsi in males $9-\mathrm{I} 2$ (usually io, average $10 \cdot 2$ ) on fore and mid tarsi, on hind tarsus 6 .
Dorsal surface of dilated apical portion of ventral arm of IX.st. of male extending farther distad than underside (Text-fig. 20), the greater portion of the long setae ventral and subventral, but in one of the four males (Text-fig. 21) the dorsal side much more convex than in the holotype (Text-fig. 20), the bristles more terminal but well below the level of the highest dorsal point. Crotchet-plate small, its margin incurved in the holotype and its lower angle with a short sharp crotchet, the outlines in the other males less distinct.

Habitat. Rabelais, near Orléansville (close to the border of Oran province), Algeria, January 1930, in nest of Meriones shawi, H. Heim de Balzac, 4 ơ (including holotype), I 9 .

## 6. Stenoponia tripectinata insperata Weiss, 1930 ; Wagner, 1932 ;

Wagner \& Wassilieff, 1933 ; Stenopia tripectinata, Jordan, I931.
The late Monsieur Weiss assumed that the left and right sides of the flea he described were identical. Counting the left-side spines and spinelets, he simply doubled the numbers; hence his statement that in the female-he described first the female and then the male, following the habit of the geneticists-the head bears a comb of 28 spines, and in the male of 26. In 1932 Wagner corrected some of Weiss's errors and added some details, but the head figured as that of a female is that of a male, and what he referred to as abdominal tergites IV and V were evidently V and VI. Fortunately Wagner sent us, in exchange, three males and four females of the series collected by Wassilieff. As Wagner used the small continental slides, the Stenoponia, like other mounted fleas received from him, were remounted at Tring and unfortunately suffered much in the process, only two of them being in fair order. Wagner's collection having been destroyed, no other specimens are available for an attempt to characterize S. tripectinata insperata.

Measurements of head : in male $\mathrm{AD}=\mathrm{BC}$ or one unit shorter, AC approximately two-fifths longer than AD (on average as $24: 17$ ) ; CD nearly as long as AC (average of $\mathrm{AD}: \mathrm{CD}$ as $17: 22$ ). Variation of genal comb in male $12 / \mathrm{I}_{3}, \mathrm{I} 3 / \mathrm{I} 2,13 / \mathrm{I}_{3}$; in female three with $14 / 14$, one with $14 / 15$, or in male $33 \%$ of combs with $12,67 \%$ with 13 ; in female $87 \%$ with 14 and $13 \%$ with 15 . Antepygidials in all three males $3 / 3$; in all four females $4 / 4$. As there is some uncertainty in the descriptions by Weiss (1930) and Wagner (1932) about the number of abdominal spinelets, particularly as regards terga IV to VI, we give here our counts in full for both sexes :

Tergite


Tergite

| II | III | IV | V | VI |
| :---: | :---: | :---: | :---: | :---: |
| $7 / 8$ | $7 / 6$ | $7 / 5$ | $2 / 4$ | $o / 0$ |
| $8 / 6$ | $7 / 5$ | $6 / 6$ | $5 / 2$ | $\mathrm{o} / \mathrm{o}$ |
| $7 / 6$ | $5 / 6$ | $6 / 3$ | $? / ?$ | $0 / 0$ |
| $9 / 5$ | $5 / 6$ | $6 / 6$ | $2 / 1 ?$ | $0 / 0$ |

Totals in male : 44, 45, 44 (average $44 \cdot 3$ ), in female: 46,46 , ?, 40 ? (average 44 ?). Variation of length of pronotum plus comb in male 29-33 units (average 3I), of metanotum 34-38 (average 36) ; in female pronotum plus comb 34-40 (average 38), metanotum 37-47 (average 42). Number of spines of pronotal comb varying in male from 33 to 35 (average 34), abdominal comb from 29 to 32 (average 3I) ; in female pronotal comb from 34 to 36 (average 35), abdominal comb from 31 to 39 (average 35). Spiniforms on apical area of underside of tarsal segment V (countable accurately on only a few tarsi) in male $7-10$ (average $8 \cdot 2$ ) on fore and mid tarsi, $6-7$ (usually 6) on hind tarsi ; in female 6 on mid tarsi, 6 (more rarely 5) on hind tarsi.

Terminalia of male: manubrium of clasper without heel, its length 22 units, digitoid (F) 27 ; dilated apex of ventral branch of IX.st. (Text-fig. 22) dorsally more convex than its ventral surface is concave, not subcircular in outline, its apical margin rounded, the long bristles below the highest point of upperside ; crotchet-plate as broad as long, its outer margin incurved, at lower angle with sharply pointed broad short crotchet, upper end without crotchet; subapical lateral lobe of paramere rounded at apex.

Habitat. Carthage area, Tunis, on Gerbillus campestris, Bir Mellah, Kairouan area, Tunisia, November 193I, on Meriones shawi (in enormous quantity in the nest according to Wagner \& Wassilieff, 1933) and Dipodillus campestris; in British Museum (Nat. History) 3 ô, 4 9.

We interpolate here, as $S$. tripectinata subsp., a pair from Biskra, South Algeria, taken by J. Steinbach on Meriones shawi in February-March igo8. The male is larger than the female and the genal combs are in the male $14 / 14$ and in the female I3/I3, from which it might be reasonable to conclude that the number of genal spines depends on the size of the specimen, which is contradicted by many instances. A pair of the next subspecies, for example, stated by the collector to have been collected on Arvicola, differ in the spines of the genal comb being in the male I4/I4 and in the female $13 / \mathbf{I 4}$, but the male is the smaller of the two, AD being i9 units long in the male and 23 in the female, the pronotum plus comb 34 in the male and 38 in the female.

Antepygidials of Biskra male 3/3, of the female $5 / 4$. Spines in pronotal comb of male 38 , of abdominal comb 38 , in female 36 and 37 respectively. Length of pronotum plus comb in male 40 units, of metanotum 44, in female 36 and 41 . Spinelets on abdominal terga in male on II $8 / 8$, III $8 / 7$, IV 6/6, V 6/4, VI o/I ; in female on II $7 / 7$, III $8 / 7$, IV 6/7, V I/I, VI o/o ; totals 54 in male, 44 in female. Spiniforms on underside of tarsal segment $V$ in male II on mid tarsus, in female 6 on fore tarsus and 5 on hind tarsus (the other tarsi imperfect or in a bad position).

Terminalia of male nearly as in S. t. insperata, dilated apex of IX.st. ventrally more rounded and expanded, but still much less convex than on dorsal side; crotchets indicated.

## 7. Stenoponia tripectinata medialis subsp. nov.

According to the accounts of S. t. insperata given by Weiss, Wagner \& Wassilieff, and the study of our seven specimens of that subspecies, the fleas we have from Rehoboth in Israel differ markedly from insperata in the genal combs, the antepygidials, abdominal spinelets and, in the female, the tarsal spiniforms.

Of our six males of medialis, two have $13 / 13$ spines in the genal combs, one has 13/I4 and three have 14/I4, none having 12 spines; put in percentages, there are $42 \%$ with 13 spines and $58 \%$ with 14 . Of the five females, one has $\mathrm{I} 3 / \mathrm{I} 3$ spines, one $\mathrm{I}_{3} / \mathrm{I}_{4}$, two $\mathrm{I} 4 / \mathrm{I} 4$ and one $\mathrm{I}_{4} / \mathrm{I}_{5}$; in percentages $30 \%$ with $\mathrm{I}_{3}$ spines, $60 \%$ with I4 and $10 \%$ with 15 . Instead of the three antepygidials found in the male of S. t. insperata and four in the female of that subspecies, there are in the six males of S. t. medialis four with $3 / 3$, one with $3 / 4$ and one $4 / 3$, and in the seven females (including two of which Professor O. Theodor has given me the details) three with $4 / 4$ bristles, two with $5 / 4$ and two with $5 / 5$, or $57 \%$ of sets of antepygidial bristles in the female with four bristles and $43 \%$ with five. Aggregate of the spinelets on abdominal terga II to VI of each male individual 43, 37, 39, 39, 35, 37 (average 38), in female $31,32,38,37,25,18,34$ (average 3I) ; the aggregate of 18 is exceptionally small and points to Subsection $\mathrm{B}^{2}$, where such low averages for the spinelets are normal. The variation in the number of spinelets on the homologous terga is as follows in the six males: on II from I2 to I4, total number 80, average I3.3, on III frorn II to 12 , total 57 , average $9 \cdot 5$, on IV from 8 to 1 , total 5 I, average $8 \cdot 5$, on V from 4 to 7 , total 29, average $4 \cdot 8$, on VI $0-2$, total 4 , average 0.67 ; in the seven females on II from 7 to 15 , total 84 , average 12 , on III from 7 to 14 , total 7 I , average 10•I, on IV from 4 to 10 , total 47 , average $6 \cdot 8$, on $V$ from o to 5 , total 17 , average $2 \cdot 4$, on VI none. Spinelets of each of the six males: on $V_{4 / 2,2 / 2,2 / 1,2 / 3,2 / 2,3 / 4 \text {, on }}$
 on VI o/o in all specimens. It should be noted that one female has no spinelets on V and that in three others one side is devoid of them, and further that the average of spinelets on segment V of the seven specimens is only one-fifth the corresponding average for segment II. The number of spines in the pronotal comb varies in the male from 31 to 34 (average $32 \cdot 7$ ) and in the female from 3 I to 36 (average 32 ); variation in the number of spines in the abdominal comb in the male is from 3 I to 36 (average $32 \cdot 3$ ), and in the female from 3 I to 39 (average $34 \cdot 4$ ). Length of pronotum plus comb in male 32-36 units (average 34) ; length of metanotum 38-42 (average 4I) ; in female pronotum inclusive of comb 36-39 units (average 37.5), metanotum 45-49 (average 46.8). Number of spiniforms on underside of tarsal segment V in male 8-12 (usually more than io) on fore and mid tarsi, 5-9 on hind tarsus (usually 6 , rarely 5), in female fore and mid tarsi with 6 (rarely 7), hind tarsus usually with 4 and less often 5 (there are also 4 spiniforms in S. t. tripectinata).
Terminalia of male similar to those of S. t. insperata, widened apical portion of
lower arm of IX.st. dorsally convex as in insperata but variable, in one male slenderer than in Text-fig. I7, broadest in male off Arvicola; crotchet shorter than outer margin of crotchet-plate.

Habitat. Rehoboth, near Jaffa, Israel, 8th February, I9I4 on Meriones shawi tristrami, and Ist January, I9I4 on "Arvicola", J. Aharoni, 6 ô, 5 우 ; holotype a male with I4/I4 spines in the genal comb, off Meriones.

Two females (one of them at Tring) from Hadassim, Israel, are referred here provisionally. Their genal combs are of $13 / 13$ and $14 / 14$ spines, their antepygidial bristles $3 / 3$ and $4 / 4$, and the totals of their abdominal spinelets 33 and 26 .

## 8. Stenoponia tripectinata spinellosa subsp. nov.

In four males and three females the variations of the proportions of the head are as follows : in male AD I8-2I units (average 19.5), AC 23-25 (average 24), BC 17-2I (average 19.3), CD 22-23 (average $22 \cdot 8$ ), BD 43-45 (average $44 \cdot 3$ ) ; in female AD 22-23 (average $22 \cdot 3$ ), AC $26-28$ (average 27), BC 23, CD 27-28 (average $27 \cdot 7$ ), BD 52 . Length of pronotum plus comb in male 30-33 (average 31.5), of metanotum 36-40 (average 38) ; in female pronotum plus comb 39-42 (average $40 \cdot 3$ ), metanotum $45-48$ (average $46 \cdot 9$ ). Spines of pronotal comb in male $34-37$ (average $35 \cdot 8$ ), in female 38 ; spines of abdominal comb in male $3 \mathrm{I}-36$ (average $34 \cdot 3$ ), in female $34-38$ (average 36) ; spiniforms on underside of tarsal segment V in male 8 (rarely 7) on fore and mid tarsi, 6-8 (usually 8) on hind tarsus ; in female 6 (more rarely 7) on fore and mid tarsi, 6 (rarely 5) on hind tarsus.

Inclusive of information received from Professor O. Theodor on additional specimens (five males, seven females) the following account is based on nine males, ten females from near the foot of Mount Carmel. One male has I2/II spines in the genal combs of the two sides, three $12 / 12$, two $13 / 12$, two $13 / 13$ and one $12 / 14$; in percentages $5.5 \%$ of combs have II spines, $56 \%$ have $12,33 \%$ I3 and $5.5 \%$ I4 spines; in the female sex one has $12 / 12$ spines, one $12 / 13$, seven $13 / 13$ and one $14 / 13$; expressed in percentages $15 \%$ of combs contain 12 spines, $80 \%$ have 13 and $5 \%$ I4 spines. The difference of 2 spines in the left and right genal combs of one of the specimens is remarkable; this condition occurs very rarely. The number of antepygidials does not vary individually, being $3 / 3$ bristles in the male and $4 / 4$ in the female. The spinelets of abdominal terga II to V are surprisingly numerous, the aggregate on each of the nine males being $49,57,45,47,52,57,55,64,59$ (average 54), in the ten females $5 \mathrm{I}, 46,50,63,54,48,68,48,64,59$ (average 55) ; similar high averages occur in the Algerian populations of S. $t$. tripectinata but the sets of antepygidial bristles in these latter nearly all contain four bristles in the male $(93 \%$ with four, only $7 \%$ with three) and all contain five bristles in the female.

Some other points of interest become very obvious when the totals of spinelets on corresponding segments are compared with each other and with the numbers in preceding populations : the variation on II in the nine males extends from $\mathrm{I}_{5}$ to $\mathrm{I}_{7}$ (total 150 ; average 16.7 ), on III from II to 17 (total 132 ; average 14.7 ), on IV from II to 14 (total II4; average $12 \cdot 7$ ), on V from 7 to II (total 77 ; average $8 \cdot 6$ ),
on VI from o to I (total 3 ; average $0 \cdot 3$ ) ; in the ten females the variation on II is from 15 to 21 (total 183 ; average $18 \cdot 3$ ), on III from 14 to 19 (total 160 ; average 16), on IV from 10 to 17 (total 140 ; average 14), on V from 5 to II (total 69 ; average $6 \cdot 9$ ), on VI always o. The female as well as the male has spinelets on both sides of tergum V, and only three of the males have only one spinelet on one side of this tergum (and six or more on the other). A comparison of the averages of the numbers of spinelets on the corresponding terga in S. t. medialis and S. t. spinellosa is given below :


Terminalia of male similar to those of S. t. medialis, but the dilated apex of the ventral arm of IX.st. a little more round-convex distally, slightly approaching symmetry.

Habitat. Mishmar Haemek (or Mishmar Ha'emeq, about 7 km . from the foot of Mt. Carmel), Israel, 7 th December, 1952, on Meriones shawi tristrami (M. Costa leg.), a series in the collection of the Department of Parasitology, Hebrew University of Jerusalem ; holotype and some paratypes in the British Museum (Natural History). Holotype a male with 12 genal spines each side, 51 abdominal spinelets and no spinelet on tergum VI. In the collection of the University of Jerusalem there are two females from near Jerusalem (Aqua Bella) which evidently belong here, but the total of abdominal spinelets in one of them is only 4 I and there is only I spinelet on tergum V .

## 9. Stenoponia tripectinata irakana subsp. nov.

The three specimens (one male, two females) we possess are characterized by the number of spines in all six genal combs being 14, and the counts of abdominal spinelets 46 in the male and 52 and 56 in the females.

Proportions of head : in both sexes AD shorter than AC, than CD and than half BD. Number of spines in pronotal comb 36 in the male, 38 and 37 in the females; in the abdominal comb 35 in the male, 35 and 38 in the females. Length of pronotum, including comb, 37 units in male, 38 and 39 in the females, of mesonotum 45 in the male, 44 and 47 in the females, of metanotum 44 in the male, 46 and 49 in the females, of abdominal tergum I inclusive of comb 35 in male, 35 and 39 in females. Antepygidials as in S. t. spinellosa, 3/3 in male, 4/4 in both females. Spiniforms on ventral surface of tarsal segment V in male II-I3 on fore tarsus, 12 on mid tarsus, 7 on hind tarsus ; females with 6 and 7 on fore and mid tarsi and 6 on hind tarsus.

Apex of ventral arm of st.IX of male almost symmetrical, proximally of the broadest point more incurved ventrally than dorsally.

Habitat. Karradit Marion, Baghdad, Iraq, 28th January, 1953, I of (type) from Mus musculus praetextus and New Baghdad Race Track, Baghdad, Iraq, 5th February, 1953, I $q$ from Gerbillus lofthusi, C. A. Hubbard; Haur al Hasa, west bank of Euphrates SW. of Faluja, Iraq, from Jaculus jaculus lofthusi, December r954, r ㅇ, D. L. Harrison.
10. Stenoponia tripectinata separata subsp. nov.

Particularly distinguished by the narrowness of the club of IX.st. of the male. Proportions of head in male : AD 19, AC 23, BC 19, CD 22, BD 42 ; in female : AD 23, AC 29, BC 21, CD 30, BD 53. Number of spines in the genal comb in males $12 / 13$ and 13/13 (type), in the only female $14 / 15$. Antepygidials $3 / 3$ in both males, $4 / 4$ in the female. Number of spinelets on abdominal terga of male holotype $7 / 7$ on II, $6 / 6$ on III, $6 / 5$ on IV, $3 / 3$ on V, none on VI (total 43), in the second male $7 / 7$ on II, $6 / 6$ on III, $5 / 6$ on IV, $4 / 4$ on V, none on VI (total 45 ) ; female with $8 / 9$ on II, $8 / 8$ on III, $6 / 6$ on IV, $3 / 4$ on V, none on VI (total 52 ). Number of spines in pronotal comb of both the male and the female from the Mersa Matruh area 36 , of the abdominal comb 32 in the male and 36 in the female; second male with 38 spines in the pronotal comb and 35 in the abdominal one. Length of pronotum plus comb in the male from the Mersa Matruh area 33 units, in the female 40 , mesonotum 38 in the male and 48 in the female, metanotum 37 in the male and 45 in the female, abdominal tergum I plus comb 29 in the male and 37 in the female; corresponding measurements in the second male 35, 40, 40 and 32 . Number of spiniforms on tarsal segment $V$ of the male holotype 12 on fore tarsus, 10 (?) on mid tarsus, 7 on hind tarsus ; female with $6,6 / 6$ and 6 respectively ; all legs of second male defective.

Club of ventral arm of IX.st. of male similar to that of S. $t$. barcana but narrower (Text-fig. 23), very little broader in second male than in holotype ; length of digitoid (F) 29 units, of manubrium (м) 26 , and of ventral margin of VIII sternum from the point of division into left and right lateral lobes proximad to the pit of the nearest long bristle 14 units, i.e. longer than in the subspecies following.

Habitat. Thirty-seven miles west of Mersa Matruh, Western Desert Province, Egypt, r3th January, r933, I of (holotype), I ㅇ, and 19 miles east of Sidi Barrani, Western Desert Province, I $\mathbf{o}^{\star}$. Both the localities are on the north-west coast of Egypt and the second locality is about 52 miles from Matruh. As the specimens were collected from burrows of undetermined rodents, by H. Hoogstraal, it seems possible that the rodent may have been Spalax ehrenbergi, which occurs from Cyrenaica (eastern Libya) through Lower Egypt to Israel and Syria.*

Subsection $\mathrm{B}^{2}$.-Head (Fig. 3) anteriorly much more rounded than in Subsection $\mathrm{B}^{1}$, the frontal angle vestigial or effaced. Oral margin, AD, as long as or longer than AC , rarely one or two units shorter than $\mathrm{AC} \dagger$. The average of the total

[^2]number of spinelets on abdominal terga II to V of the specimens of a subspecies is 30 or less; VI without spinelets in either sex. Club of IX.st. of male almost symmetrical as in S. t. insperata and S. t. irakana. Three subspecies.

Group $b^{4}$.-Number of spines of the genal comb in the majority of specimens of both sexes 14, none of either sex with 16 . Abdominal tergum V in both sexes with one or two spinelets on at least one side. Average totals of spinelets in our two males 29, in three females 29.3 ; average number of spinelets on IV in male 6, in female $6 \cdot 7$.

## II. Stenoponia tripectinata blanda subsp. nov.

Proportions of head in male holotype (those for male paratype in brackets) : AD I8 units (2I), AC I9 (20), BC I7 (I9), CD 23 (24), BD 40 (43). In three females $\mathrm{AD} 20,2 \mathrm{I}$ and 22 respectively, $\mathrm{AC} 2 \mathrm{I}, 2 \mathrm{I}$ and $22, \mathrm{BC} 19,20$ and $2 \mathrm{I}, \mathrm{CD} 23,25$ and 26 , BD 43, 45 and 46 . Spinelets on abdominal terga in holotype male $7 / 6$ on II, 6/5 on III, $4 / 4$ on IV, $\mathrm{o} / \mathrm{I}$ on V, total 33 ; in second male $5 / 6,4 / 4,2 / 2$ and $\mathrm{I} / \mathrm{I}$, total 25 ; average total number of spinelets for the two males 29 . Spinelets in the three females $6 / 5,5 / 6$ and $6 / 6$ on II, $4 / 4,4 / 5$ and $7 / 5$ on III, $2 / 3,3 / 3$ and $5 / 4$ on IV, o/I, I/I and o/2 on V, totals for the three individuals 25,28 and 35 (average 29.3). The aggregate number of spinelets on tergum IV of the two males is I2 (average 6) and in the three females the aggregate is 20 (average $6 \cdot 7$ ), while in the two subspecies which follow the average number of spinelets on IV is half (male) or less than half (female) the number found in blanda. Spines of pronotal comb of male $15 / 15$ and 17/17, in females $18 / 18,18 / 17$ and $17 / 19$. Dorsal length in males of pronotum plus comb 28 and 30 , of mesonotum 34 and 36 , of metanotum 36 in both, of tergum I of abdomen including comb 28 and 30 ; corresponding figures for the three females are pronotum with comb 33, 32 and 30 , mesonotum 41,40 and 35 , metanotum 42 , 40 and 37 , tergum I with comb 35,35 and 34 . Number of spiniforms on apical area of underside of tarsal segment V in males?/? and $8 / 9$ on fore tarsus, $7 / 7$ and ?/? on mid tarsus, $6 / 6$ and $6 / 6$ on hind tarsus; in females ?/?, $6 / 7$ and ?/6 on fore tarsus, $7 / 6$, ?/6 and $6 / 6$ on mid tarsus, $6 / 6,6 /$ ? and $6 / 6$ on hind tarsus.

The length of the convex dorsal surface of the club of IX.st. of male (measured from upper long apical bristle forward) is nearly equal to width of club and the concave ventral area extends to the first long ventral bristle of the apical row.

Habitat. Bir Bosslanga, near Salum (or Sollum), Libyan Plateau, Western Desert Province, Egypt, about 500 ft., from nests of Gerbillus, 25th October, 1953, H. Hoogstraal, I đ (the holotype) and 3 우 12 miles south of Sidi Barrani, Western Desert Province, from Gerbillus gerbillus, 23rd April, 1954, H. Hoogstraal, I ${ }^{\star}$.

The form is morphologically intermediate between the preceding subspecies and the following ones.

Group $b^{5}$.-The number of spines in the genal combs is 15 or 16 in the great majority of males, in females it is $15, \mathrm{I} 6$ or (rarely) 17 . The total number of spinelets on the abdominal terga varies in the thirty-five males seen from 9 to 24 (average 15 ), in the fifty-one females from II to 27 (average
20.5). There are two subspecies, possibly more. We have five males and six females from Ain Séfra, South-west Oran near the Moroccan border, sixteen males and twenty-five females from Egypt (mostly from Giza Province and the adjacent portion of Beheira Province, but also some from north of Shirbin) and Israel (two pairs from near Tel-Aviv plus detailed information of twelve males and sixteen females supplied by Prof. Theodor). The Stenoponia in question are almost confined to Gerbillus and Jaculus, which are partial to sand-dunes; it is a reasonable assumption that Stenoponia will be found in suitable places everywhere from Morocco (inclusive) to Egypt as well as in the Arab countries of the Middle East.

## 12. Stenoponia tripectinata thinophila subsp. nov.

Variation of proportions of head in five males : AD 22-26 units (average 22.8), AC 20-23 (average $2 \mathrm{I} \cdot 6$ ), BC 18-2I (average 19.0), CD 24-29 (average $26 \cdot 0$ ), BD $45-50$ (average $46 \cdot 2$ ) ; in six females AD 23-26 (average 24.2), AC 23-26 (average 24.3), BC $20-22$ (average $21 \cdot 4$ ), CD $28-35$ (average $30 \cdot 8$ ), BD $52-56$ (average $54^{\circ}$ ). Variation in the left and right sides of the genal comb in males : $14 / \mathrm{I} 3, \mathrm{I} 4 / \mathrm{I} 4, \mathrm{I} 4 / \mathrm{I} 4$, $15 / \mathrm{I} 4, \mathrm{I} 6 / \mathrm{I} 5$; in females $\mathrm{I} / \mathrm{I} 5, \mathrm{I} 5 / \mathrm{I} 6,15 / \mathrm{I} 6, \mathrm{I} 6 / \mathrm{I} 6,16 / \mathrm{I} 6, \mathrm{I} 6 / \mathrm{I} 6$; in the males $10 \%$ of combs with 13 spines, $60 \%$ with $14,20 \%$ with 15 and $10 \%$ with 16 ; in the female $33.3 \%$ with 15 spines and $66.7 \%$ with 16 ; the high proportion of genal combs with 14 spines in the male and 16 in the female is characteristic of this subspecies. Antepygidial bristles: four males with $3 / 3$ and one with $4 / 4$ (i.e. $80 \%$ with three bristles and $20 \%$ with four), two females with $4 / 4$ and four with $5 / 5$ (i.e. $33 \cdot 3 \%$ with four and $66.7 \%$ with five). As the abdominal spinelets are of special interest in the study of the evolution of the S. tripectinata complex and our eleven specimens are a mere sample from an isolated locality in western Algeria, the details of the variation of the spinelets are given here as a possible help for the future student of these fleas who may have abundant material from the areas further west and east which are not at present accessible to the naturalist.


Average of individual totals of spinelets in male $16 \cdot 6$, in female $18 \cdot \mathrm{I}$. In the five males total of spinelets on II 46 (average $9^{\cdot 2}$ ), on III 25 (average $5^{\circ}$ ), on IV 12

[^3](average $2 \cdot 4$ ), on V I (average $0 \cdot 2$ ) ; in six females 54 on II (average $9 \cdot 0$ ), 27 on III (average $4 \cdot 5$ ), 2 I on IV (average $3 \cdot 5$ ), 7 on V (average $\mathrm{I} \cdot 2$ ). The present population differs from all others in the fact that tergum $V$ bears spinelets in four out of six females, whereas in the male only one specimen has a spinelet on V. In the two following populations (thirty males and forty-five females in all) one male has spinelets on V and all females are without them on this tergum.

Number of spines in pronotal and abdominal combs in individual males 39 and 38, 33 and 34,34 and 30,35 and 35,35 and 36 ; in females 37 and 39,38 and 43,37 and 42,39 and $4 \mathrm{I}, 38$ and 42,35 and 35 ; averages in male $35 \cdot 6$ and $34 \cdot 6$, in female 34.4 and $37^{\circ} 0$. The fact that in the female the number of spines in the abdominal comb is nearly always greater than the number in the pronotal comb is the opposite of what obtains in the populations of Group b ${ }^{\mathbf{5}}$ from Egypt and Israel.

Lengths of various segments are as follows:

|  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Pronotum plus comb | Mesonotum | Metanotum | Abdominal t.I plus comb |
|  | $3^{6}$ | 39 | 4 I | 34 |
|  | 30 | 36 | 35 | 29 |
|  | 29 | 33 | 33 | 28 |
|  | 30 | 36 | 37 | 32 |
|  | 29 | 33 | 36 | 30 |
| Average | $30 \cdot 8$ | $35 \cdot 4$ | $36 \cdot 4$ | $30 \cdot 6$ |
|  | - |  |  | $\square$ |
|  | 38 | 45 | 43 | 39 |
|  | 37 | 42 | 45 | 40 |
|  | 40 | 47 | 48 | $4{ }^{1}$ |
|  | 39 | 43 | 43 | 40 |
|  | 37 | 45 | 42 | 37 |
|  | 36 | 43 | 42 | 38 |
| Average | $37 \cdot 8$ | $43 \cdot 6$ | $43 \cdot 8$ | $39^{2}$ |

Number of spiniforms on apical area of underside of tarsal segment V of male on the two sides ?/9, ?/8,?/9, I4/?, $8 /$ ? on the fore tarsus, ?/9, $9 /$ ?, $8 / ?, ? / ?, 8 / 7$ on the mid tarsus and $7 / 7, ? / ?, ? / 7,8 / 8,6 /$ ? on hind tarsus ; females with ? / $8,7 / 8,7 / 7,8 / ?$, $7 / 7$ and ?/? on fore tarsus, ?/7, $7 /$ ?, $7 / ?, 8 / 7,7 /$ ? and $9 / 9$ on mid tarsus and ?/7, 6/?, $6 / 6$, ?/6 and ?/5 on hind tarsus.

The convex dorsal surface of the club of IX.st. of the male longer than in the next subspecies and the underside, from the long apical bristles forward, usually a little more distinctly convex than in Text-fig. 24, taken from the type.

Habitat. Ain-Séfra, south-western portion of Province of Oran, Algeria, 4th-7th May, 1913, from Gerbillus pyramidum hirtipes, Dunn leg. (on ornithological expedition of W. Rothschild and E. Hartert to western Algeria), 5 ot and 6 \& . Holotype a male with $\mathrm{I} 4 / \mathrm{I} 4$ genal spines and $2 / \mathrm{I}$ spinelets on tergum IV.
13. Stenoponia tripectinata acmaea subsp. nov.

The typical area of this subspecies is the Giza Province, on the west bank of the Nile opposite Cairo, extending west to the pyramids of Rawash and northwards over the southern border of the Beheira Province at El Khataba (or Khâtabba). A male from 40 km . west of Cairo has the abdomen so much contracted that the spinelets of terga IV and V cannot be studied; the specimen may represent a cline towards S. t. blanda. The four specimens obtained by H. Hoogstraal far north, at Kafr el Battik, almost opposite Damietta (now Dumyat), are also better considered as atypical on account of the fact that the single male has I3 spines in the left genal comb and 15 in the right one, a degree of lopsidedness otherwise occurring only in Israel. The large area of lowland traversed by freshwater channels lying to the north and east of Cairo and including the Land of Goshen (where Pharaoh settled the family of Joseph) is as far as Stenoponia is concerned a blank. Excluding these atypical specimens, the material consists of fourteen males and twenty-two females.

The averages of the measurements of the head in the fourteen males are : AD 24.5 , AC 22.4 , BC $20 \cdot 6$, CD $27 \cdot 5$, BD $48 \cdot 0$, and in the twenty-two females $\mathrm{AD} 26 \cdot 7$, $\mathrm{AC} 24 \cdot 5$, $\mathrm{BC} 2 \mathrm{I} \cdot 3, \mathrm{CD} 30.7$ and BD 53.5 . As samples of the individual variation, the measurements of the two males and two females, of which one specimen of each sex has the longest measurement for AD and the other the shortest, are recorded : the measurements for these four specimens being for the male sex AD 27 and $22, \mathrm{AC} 23$ and 21 , BC 18 and $18, \mathrm{CD} 29$ and 26 , and BD 50 and 45 ; in the female sex AD is 29 and 24 , AC 26 and 24, BC 2 I and 2I, CD 3 I and 29 and BD 54 and 50 . The number of spines in the genal combs varies in the males from $\mathrm{I}_{4}$ to I 6 and in the females from 14 to 17, the percentages being in the male sex $21.4 \%$ of combs with 14 spines, $64 \cdot 3 \%$ with 15 and $14 \cdot 3 \%$ with 16 , in the female $2 \cdot 3 \%$ (one comb only) with 14 spines, $54.5 \%$ with $15,38.7 \%$ with 16 and $4.5 \%$ with 17 spines; the number of specimens in which the number of spines in the left and right combs differs by one spine is remarkably high, eight males and nine females (seventeen of the thirty-six specimens, or $47.2 \%$ ) having this asymmetrical arrangement. The holotype is a specimen with 15 spines each side.

The sets of antepygidial bristles consist in the male of three or four bristles and in the female four or five, in the male $67 \cdot 9 \%$ of the sets with three bristles and $32 \cdot \mathrm{I} \%$ with four, in the female $25 \%$ of the sets with four bristles and $75 \%$ with five; it is rather surprising, and perhaps not a coincidence, that in the three males and three females with asymmetrical sets of antepygidials it is the left set which has a bristle less than the right, whereas in the asymmetrical antepygidial sets of the male from 40 km , west of Cairo, the male and one female from north of Shirbin, and a male of S. $t$. blanda it is the right side which has a bristle less. The average number of spines in the pronotal comb is 36.4 in the male and 38.4 in the female, and of the abdominal comb 35.5 in the male and 37.5 in the female; frequently the pronotal comb has one or a few spines more than the abdominal comb, but the reverse also occurs.

Certain measurements (in units) of the thoracic nota and abdominal tergum I,
together with averages (in brackets) in fourteen males and twenty-two females are given below :-

|  |  | Pronotum | Mesonotum | Metanotum | Abdominal |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Variation in ${ }^{*}$ |  | $\begin{gathered} 30-36 \\ (\operatorname{av.} 33 \cdot 0) \end{gathered}$ | $\begin{gathered} 35-4 \mathrm{I} \\ (\text { av. } 36 \cdot 8) \end{gathered}$ | $\begin{gathered} 35-4 \mathrm{r} \\ (\text { av. } 38 \cdot 8) \end{gathered}$ | $\begin{gathered} 28-35 \\ (\operatorname{av} .32 \cdot 6) \end{gathered}$ |
| Variation in 9 |  | $\begin{gathered} 33-40 \\ \text { (av. } 37 \cdot 9 \text { ) } \end{gathered}$ | $\begin{gathered} 40-47 \\ (\operatorname{av.} .44 \cdot 4) \end{gathered}$ | $\begin{gathered} 40-47 \\ \left(\operatorname{av} .44^{\circ} 4\right) \end{gathered}$ | $\begin{gathered} 34-40 \\ (\mathrm{av} \cdot 37 \cdot 9) \end{gathered}$ |
| Length in $\delta^{*}$ with longest pronotum |  | 36 | 40 | 4 I | 34 |
| Length in $\hat{0}$ with shortest pronotum |  | 30 | 36 | 36 | 30 |
| Length in $¢$ with longest pronotum. |  | 40 | 47 | 47 | 41 |
| Length in $q+$ with shortest pronotum |  | 33 | 46 | 46 | 40 |

The totals of abdominal spinelets of individuals vary in the male from 14 to 24 (average 20) and in the female from io to 26 (average 19). Counts of the spinelets on segments II to V of the two males with the highest and lowest total numbers are I3 and 9 on II, 8 and 4 on III, 3 and I on IV and o and o on V ; corresponding counts for females are I4 and 6 on II, 8 and 4 on III, 4 and o on IV and o and o on V. The aggregate number of spinelets on the individual terga in the fourteen males is 150 on II (average 10.7), 85 on III (average 6.1), 39 on IV (average $2 \cdot 8$ ) and 2 on V (average $0 \cdot 14$ ) ; in the twenty-two females the aggregates are 240 on II (average $10 \cdot 9$ ), 137 on III (average $6 \cdot 2$ ), 40 on IV (average $\mathrm{I} \cdot 8$ ) and o on V. All the males have at least onc spinelet on IV, whereas among the females there are four specimens in which IV has no spinelets; the greater reduction in the female of spinelets on IV and the retention in one male of spinelets on V are in accord with the general trend of evolution in the tripectinata complex, the female being a step in advance of the male.

The spiniforms on the apical area of the underside of tarsal segment V can be counted in half the tarsi of the fourteen males ( 42 out of 84 ) and nearly half those of the twenty-two females ( 64 out of 132) ; the counts vary in the males from 6 to 9 and in the females from 6 to 8 , the most interesting fact being some high counts on the hind tarsus of females. Of the males, one fore tarsus has 7 , seven have 8, three have 9 (average $8 \cdot 2$ ), three mid tarsi have 7 , six have 8 , and one has 9 (average $7 \cdot 8$ ), seven hind tarsi have 6 , ten have 7 , three have 8 and one has 9 (average $6 \cdot 9$ ); in the females two fore tarsi have 6 , eight have 7 , and six have 8 (average $7 \cdot 3$ ), one mid tarsus has 6 , eighteen have 7 and five have 8 (average $7 \cdot 2$ ), twelve hind tarsi have 6 , seven have 7 and five have 8 (average $6 \cdot 7$ ).

The club of the ninth sternite of the male (Text-fig. 25) is nearly as convex below as above, its outline approaching symmetry. There is nothing in the clasper and phallosome distinguishing the present subspecies (Text-fig. 30).
Habitat. Abu Rawash, Giza Province, Egypt, 18th March, 1952, in Arvicanthis nest 2 ó, 2 우: El Mansuriya, Giza Province, 3rd April, 1952, from nest of Gerbillus gerbillus, 4 ठ̃, 6 웅 Mansuriya, Giza Prov., edge of desert, from rodent's nest, December 1951, 2 우: Beni Salama, Giza Prov., 29th January, 1953, from Gerbillus burrow, Iơ ; Abu Ghâlib, Imbaba, Giza Prov., 2nd May, 195I, from nest of Gerbillus gerbillus, I 9 ; Kafr Hakim, Imbaba, Giza Prov., 6th February, 1953, from Gerbillus burrow, I ô, I ¢ ㅇ Mansuriya, Imbaba, Giza Prov., 12th February, 1953, from

Gerbillus gerbillus (probably a nest), $2 \widehat{\jmath}$ (including the holotype), i $q$; Mansuriya, Imbaba, Giza Prov., 9th March, 1953, from Jaculus jaculus, I 9 ; Afifi Pasha, Ezbet Hafiz, Giza Prov., 29th March, 1952, from nest of Jaculus jaculus, 3 d ${ }^{\text {T, }} 6$; ; El Khataba (or Khâtabba, a short distance north of Giza Prov.), Beheira Province, 29th January, I953, from Gerbillus nest, I ot, 2 우.


Fig. 30. Terminalia of male paratype of Stenoponia tripectinata acmaea ssp. nov.
The male from the Western Desert Province, 40 km . west of Cairo, Ist April, 1952, and the male and three females from Kafr el Battik, north of Shirbin, Gharbiya Province, February 1953, may provisionally be referred to as S. t. acmaea var. or cline.

The last remark applies likewise to the Palestinian specimens similar to S. $t$. acmaea of which Dr. O. Theodor has sent us two pairs and particulars of many other specimens. All the localities of these specimens are in or near the sand-dunes from a little north of Tel-Aviv southwards, as follows: Herzliah (about 15 km . north of Tel-Aviv), from Gerbillus gerbillus, one male, one female, Cholon (or Holon),
just south of Tel-Aviv, from Gerbillus pyramidum and G. gerbillus, two pairs received from Dr. Theodor with details of two other pairs, Nahr Rubin, two males, two females, Rishon Lezion, from Meriones crassus sacramenti. G. pyramidum and G. gerbillus, six males, three females, Ashkelon, from Gerbillus, one male, Beersheba, from G. pyramidum, three males, six females, Revivim, 30 km . south of Beersheba, from G. pyramidum (rarely on Meriones c. crassus), four males, eight females. In these twenty-one males and twenty-four females the averages of the totals of the spinelets on abdominal terga II to V vary from 2I down to II ; there is only one specimen (a male) with a spinelet on V . In the males $97 \cdot 6 \%$ of sets of antepygidial bristles consist of three and $2.4 \%$ of four, and the percentage with three would be $100 \%$ if the Herzliah male were excluded, in the females $35.4 \%$ of sets have four bristles and $64.6 \%$ are of five ; in the male sex of these Palestinian specimens the percentages differ remarkably from those of typical S. t. acmaea. The number of spines in the genal comb varies in the males from 13 to 16 and in the females from I4 to I7; in the males $4.8 \%$ have I3 spines, $45.2 \%$ have $14,40.5 \%$ have $I_{5}$ and $9.5 \%$ have 16 , the specimens with 13 and 14 spines in the combs of the two sides (Cholon and Rishon) are not matched in typical S. t. acmaea; in the females $12.5 \%$ of combs are of 14 spines, $64.5 \%$ of $15,18 \cdot 8 \%$ of 16 and $4.2 \%$ of I7 spines, combs with 14 and 15 spines being more numerous than in S. t. acmaea and those with 16 spines correspondingly less numerous. A more striking point, however, is the occurrence in the material from Israel of three further specimens with 2 more spines on one side of the head than on the other, a condition found only twice before. That these five cases of an unusual degree of lopsidedness, occurring in one Egyptian male (Gharbiya Province, north-eastern area of the Nile delta, with 13/15 spines), three males from Israel (foot of Mt. Carmel, with I2/I4 spines, Beersheba, with $16 / 14$ spines, and Revivim, with $14 / 16$ ) and one female from Israel (Nahr Rubin, with $17 / 15$ spines) are all from one small corner of the Middle East and nowhere else can hardly be accidental. Chiefly for comparison with S. t. acmaea we gave above the percentage of occurrence of various numbers of spines in the genal comb. Statistical facts of another kind arise from a comparison of the totals of genal spines on the two sides of each individual in the twenty-four females from Israel of the form resembling S. $t$. acmaea: the combination $14 / \mathrm{I} 4=28$ spines occurs once, $\mathrm{I}_{4} / \mathrm{I}_{5}$ or $\mathrm{I}_{5} / \mathrm{I}_{4}=29$ spines twice each, $\mathrm{I}_{5} / \mathrm{I}_{5}=30$ eleven times, $\mathrm{I}_{5} / \mathrm{I}_{5}$ and $16 / 15=31$ three times and once respectively, $16 / 16=32$ twice, $17 / 16=33$ once and $17 / 15=32$ once. In other words, while uneven totals (29, 31 and 33) must represent heads with the number of spines in the genal combs of the two sides different, even totals may mean either that the counts on the two sides are the same $(14 / 14=28,15 / 15=30,16 / \mathrm{I} 6=32)$ or that the combs are very strongly asymmetrical ( $17 / 15$ in the female, $14 / 16$ and $16 / 14$ in males). Out of these twenty-four females, fifteen have an even number of spines in the genal combs of the two sides together, while in ten specimens the number of spines on the two sides is different.

Though the proportion of symmetrical and asymmetrical heads varies in different populations of the tripectinata-complex, in every such population more than half the individuals have even totals of genal spines on the two sides together.

The number and position of the genal spines are the result of two obvious main
lines of evolution which are interdependent. The reduction of the abdominal spinelets in a forward direction reaches its maximum in the absence of spinelets on terga VI, V and IV in one individual of S. t. acmaea and in three from Israel, which suggests the possibility that there may be some place in the Middle East where tergum IV is without spinelets in all individuals. This reduction of the spinelets probably increases the amount of material available for forming the spines of the genal comb and thus helps to increase the number of them along the antennal fossa, the acme of this upward development bringing the uppermost spine close to the eye ; the black stripe from the eye upwards (the trabecula centralis of Wagner) is the place where the left and right sides of the head are united and its presence may prevent any further development upwards of the comb in Stenoponia, in which the highest combination yet known is $16 / 16$ spines in the male and $16 / \mathrm{I}_{7}$ (and $\mathrm{I}_{7} / \mathrm{I} 6$ ) in the female, $17 / \mathrm{I} 7$ being as yet unknown. As the Siphonaptera are holometabolous, the division, for forming the organs of the imago, of the material accumulated during the larval life takes place in the last larval stage and in the pupa under the control of the system of collaborating endocrines discovered by biochemists, the control continuing the orderliness which the taxonomic unit (in this case S. t. acmaea together with the acmaea-like specimens from Israel) has acquired in its evolution. In rather more than one-third of the specimens the left and right genal combs differ by one spine ; the endocrinal " board of control " is " accustomed " (so to speak) to pass this difference as correct, but when provided with material for an evennumbered division the error may occur that the line of division is one spine to the right or left, resulting in the strongly asymmetrical arrangement I4/I6 or I6/I4. It is possible that this combination may injuriously affect the viability of the specimen, which will die in the pupa or soon after emerging and thus rarely come into the hands of the collector. Whether this suggestion is correct or not, it does not account for the occurrence of the error only in one small area of the Middle East.

When eight specimens from Morocco with the same number of spines in the genal comb of each side of each individual were considered under S. t. megaera on p. 186, the question was put whether a series with symmetrical heads is taxonomically the same as a series from another locality in which the heads are often asymmetrical; if $13 / I_{3}$ must be considered the same as $14 / I 4$, specimens with the combinations $\mathrm{I}_{3} / \mathrm{I}_{4}$ and $14 / \mathrm{I}_{3}$ belong to the same subspecies provided there are no other differences. Another question which was touched upon under S. t. insperata, on p. 189, is whether the number of genal spines depends on the size of the specimen; measurements show that, though the smallest specimens within a subspecies do not have the maximum counts nor the largest the smallest ones, yet the specimen with the greatest number of spines is not necessarily the largest while the one with the smallest number of spines is not always the smallest specimen ; in S. t. acmaea, for instance, the largest specimen was a female with $15 / \mathrm{I}_{5}$ spines in the genal combs, while specimens with $16 / 17$ and $17 / \mathrm{I} 6$ were smaller.

The spinelets of the abdominal terga vary much in size and number. Most of them are triangular and at least twice as long as broad. In one specimen tergum II bears dorsally on the left side 3 spinelets of which 2 are broken off but the third is intact, shaped like the spines of the abdominal comb but much shorter. In three
specimens one of the terga has either on the left or right side a dark spine, shaped like a cigar and about half the length of the longest lateral spine of the abdominal comb, which is stuck by its broad end to the apical margin of the tergum. I look upon this as a remnant of spine-substance which was left over when all the spines and spinelets were formed and of which the metabolic factors disposed in this way.

The conspicuous asymmetry of the genal combs is repeated by the antepygidial bristles, evidently independently of the asymmetry of the genal combs. In all our specimens in which the sets of antepygidial bristles are asymmetrical the difference between left and right is one bristle, but Dr. V. E. Tiflov has discovered in one male of $S$. ivanovi a count of 4 antepygidials on the left side and only 2 on the right, and in a female of $S$. suknevi a count of 5 and 7 on the two sides.

## SUMMARY

In this paper the genus Stenoponia has been divided into two sections. Section A contains eleven species, which have been grouped into defined subsections and the main distinctions of each species have been mentioned ; two of these species are Nearctic and the remainder are from the eastern portion (Siberian and Manchurian subregions) of the Palaearctic. Section B contains a single species, S. tripectinata, which occurs in the Mediterranean subregion and breaks up into numerous subspecies of which eleven have been described as new in this paper. All populations of this species are very variable and even the left and right sides of the same specimen are never exactly alike. These populations show two obvious lines of evolution which are interdependent: ( I ) development of the genal comb upwards along the margin of the antennal fossa (accompanied by an increase in the number of its spines) until the uppermost spine is close to the vestigial eye, and (2) a decrease in the number of marginal spinelets on the abdominal terga which takes place progressively from tergum VI forwards until VI and V (also IV in a few specimens) are without spinelets. More than half the specimens of S. tripectinata have the same number of spines in the genal combs of the two sides, but many have one spine more in the comb of one side than in that of the other and a few specimens (all from one area comprising part of Israel and an almost adjacent portion of northern Egypt) have a difference of two spines in the genal combs of the two sides. The number of antepygidial bristles varies independently in a similar manner.

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[^0]:    * One unit equals approximately $10 \mu$.

[^1]:    * The position of segment $V$ on the slide is more often unfavourable than favourable for the exact counting of the spiniforms, the numbers of spiniforms are usually higher in males than in females and on fore and mid tarsi than on hind tarsus.

[^2]:    * Mr. Hoogstraal kindly tells us that he thinks the very characteristic burrows of Spalax would have been recognized and that it is more probable that the owners of the burrows were either Meriones shawi or Psammomys obesus.
    $\dagger$ It is sometimes necessary to measure both sides of the head and take the average of these measurements as the true length.

[^3]:    * The great difference in the number of spinelets on the left and right sides of this specimen is partly due to unsatisfactory mounting, the sides not covering each other symmetrically so that the two spiracles of a segment are as far apart vertically as double the interspace between two long bristles of the posterior row.

